

New zyglodopodons from Miocene of China and their taxonomy

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Abstract The zygodont proboscideans from the Miocene strata of China are widely distributed. However, the materials are scarce, and their classification has experienced a longtime controversy, from the chaotic state of multiple *Zygodont* species to the only one species, *Zygodont gobiensis*. The combined species *Z. gobiensis* comprises both the gracile type with a high degree of zygodonty and the robust type that is between the typical bunodont and zygodont morphology. Recently, as the robust type has been re-allocated to another genus *Miomastodon* and new fossil remains were discovered, it is necessary to further evaluate and classify the zygodont proboscideans from the Miocene of China. In the present paper, we restudied the previously published zygodont specimens of the gracile type, as well as several unpublished *Mammutidae* specimens. The former including *Z. nemonguensis*, *Z. gromovae*, *Z. jiningensis*, *Z. chinjiensis* and two specimens of *Gomphotherium xiaolongtanensis*, represents *Zygodont* in the original sense in China. In these specimens, the tip of the loph(id)s are sharp. The anterior and posterior pretrite central conules are absent or very weak, and the anterior and posterior crescentoids are sharp and slender. The posttrite mesoconelets are well subdivided and the zygodont crests are developed. In buccal view, the loph(id)s are “Λ-shaped” and the interloph(id)s are “V-shaped”. Their molar morphology resembles that of *Z. turicensis*, and hereby, they were identified as *Zygodont* cf. *Z. turicensis*. Several unpublished specimens from Hezheng, Gansu, Tonggur, Nei Mongol, Tongxin, Ningxia and Junggar, Xinjiang exhibit a lower degree of zygodonty, corresponding to the “robust type of *Zygodont*” in which the molar morphology is between the typical bunodonts and zygodonts. The pretrite crescentoids are thicker than *Zygodont* cf. *Z. turicensis*, and the pretrite central conules usually present on the first and second interloph(id)s. According to the stratigraphic age and characteristics, two species, *Miomastodon gobiensis* and *Mio. tongxinensis* were identified. The anterior and posterior pretrite crescentoids of *Mio. tongxinensis* are weaker and the pretrite central conules are larger than *Mio.*

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gobiensis. Geographical distribution indicates that *Miomastodon* is the predominant member of zygodonts in the Early and Middle Miocene in northern China. The discovery of new materials and the reclassification of zygodonts provide further evidence for dispersal of Mammutidae from Eurasia to North America and the evolutionary relationships among the species of the family Mammutidae in China.

Key words China, Miocene, Mammutidae, *Zygodont*, *Miomastodon*

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1 Introduction

Mammutidae is one of the two main branches of Elephantiforms with the same meaning of zygodont mastodonts. This group has a wide geographical distribution. Spatially, they have been discovered from all continents except Antarctica, Oceania, and South America, and temporarily they ranged from the Late Oligocene to the end of the Pleistocene. According to current research, the Mammutidae contains 6 genera: *Losodokodon* Rasmussen & Gutierrez, 2009, *Eozygodon* Tassy & Pickford, 1983, *Zygodont* Vacek, 1877, *Miomastodon* Osborn, 1922, *Mammut* Blumenbach, 1799, and *Sinomammut* Mothé et al., 2016 (Shoshani and Tassy, 2005; Rasmussen and Gutierrez, 2009; Mothé et al., 2016; Wang et al., 2020). In China, although 5 of the 6 genera (except *Losodokodon*) has been reported, fossil mammutids are scarce, except for the Yushe Basin, Shanxi Province, where *Mammut borsoni* were rich and well-preserved from the Late Miocene to Pliocene.

Zygodont is another genus frequently reported in China, and the age is earlier than that of *Mammut*. The materials were mainly discovered from the Miocene localities of northern China, such as Tunggur, Junggar, Tongxin, Linxia, as well as scattered materials from southern China. Because the most remains were isolated cheek teeth with ambiguous provenance, the classification is always in controversy. Tobien et al. (1988) attributed all remains to one species, *Z. gobiensis*. However, the tooth morphic-types of *Z. gobiensis* sensu Tobien et al. (1988) include not only typical zygodont type, but also some intermediate forms between gomphotheres and mammutids.

In the recent years, benefiting from the discovery of new materials and the development of biostratigraphy, re-study of *Zygodont* from China is imperative. Wang et al. (2020) attributed the untypical zygodonts (intermediate morpho-type between zygodonts and bunodonts) into *Miomastodon*, and the typical zygodonts should be retained in the genus *Zygodont* (close to *Z. turicensis*). In the present article, we will further discuss the new materials of *Zygodont* and *Miomastodon* from Miocene of China.

Materials and methods The new materials reported herein include an incomplete mandible (1986-NMG-DM) from the Damiao locality, Nei Mongol (Inner Mongolia), which is housed in the Inner Mongolia Museum. A complete right m3 (IVPP V26615) collected

by Chen Guan-Fang from Tunggur Formation at Nei Mongol is housed in IVPP. Three specimens housed in HNV, include a broken mandible (HNV1808) from the Hujialiang Formation at Laogou locality, Gansu; a right M3 (HNV1938) and a right M2 (HNV1939) from the Linxia Basin, but the precise locality is unknown. A right M3 (IVPP V26803) is from Tongxin, Ningxia, and the precise locality is probably Dingjiaergou, Zhangenbao Formation. An incomplete right M3 (IVPP V30715) was discovered by Wang Shi-Qi from the Halamagai Formation of the Junggar Basin, Xinjiang. The above specimens were attributed to *Miomastodon*.

A left m3 (IVPP V26802) presented by Daiyuan Primary School of Luonan County, Shaanxi Province, is currently stored in the IVPP. The precise locality is unknown. It was attributed to *Zygodont*. Furthermore, the previously published zygodont materials that can be attributed to *Zygodont* and *Miomastodon* from China were also reevaluated.

The terminology of occlusal structures of zygodont cheek teeth follows Wang et al. (2020). The terminology of mandibular anatomical structure follows Tassy (2013). The measurements of mandibles and cheek teeth follow Tassy (2013, 2014) and were obtained using callipers (in mm).

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; GPM, Gansu Provincial Museum, Lanzhou, China; HNV, Hezheng Paleozoological Museum, Hezheng, Gansu, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; PIN, Paleontological Institute, Moscow, Russia; THP, Tianjin Natural History Museum, Tianjin, China.

2 Systematic paleontology

Order Proboscidea Illiger, 1811

Family Mammutidae Hay, 1922

Genus *Zygodont* Vacek, 1877

Type species *Zygodont turicensis* (Schinz, 1824)

Diagnosis The tooth loph(id)s are antero-posteriorly compressed with a sharp cutting edge in the fresh molar. The lophs of upper cheek teeth are perpendicular to the median sulcus, and the lophids of lower cheek teeth are oblique to the median sulcus. The anterior and posterior pretrite central conules are disappeared or very weak. In the fresh molars, the anterior and posterior pretrite crescentoids display fine serrated knobs, and exhibit thin crests after slight wear. The pretrite mesoconelets are also subdivided and crest-like. The posttrite half loph(id)s display a high degree of subdividing, and the zygodont crests are developed. The interloph(id)s are open, not obstructed by the crescentoids. The anterior and posterior pretrite crescentoids almost reach the bottom of the interloph(id)s. In lateral views, the loph(id)s are “Λ-shaped”, and the interloph(id)s are deep “V-shaped”.

Referred species *Zygodolophodon aegyptensis* (Sanders and Miller, 2002); *Z. atavus* (Borissiak, 1936).

***Zygodolophodon* cf. *Z. turicensis* (Schinz, 1824)**

(Fig. 1; Table 1)

- Zygodolophodon* (*Turicus*) *nemonguensis* Chow and Chang, 1961, p. 249–250, pl. 2, 3, figs. 4, 4a
Zygodolophodon gromovae Dubrovo, 1970, p. 136–138, figs. 1, 2
Zygodolophodon jiningensis Chow and Chang, 1974, p. 35–36, pl. 15, figs. 1, 1a
Zygodolophodon chinjiensis (Osborn, 1929) Chow et al., 1978, p. 71–72, pl. 8, figs. 1, 2
Gomphotherium xiaolongtanensis Chow and Chang, 1974, p. 24, pl. 5, fig. 2
Zygodolophodon gobiensis (Osborn and Granger, 1932) Tobien et al., 1988, p. 149, 151, 153, 154, figs. 40, 42, 45, 46; Chen, 2021, p. 20–22, fig. 9
? *Zygodolophodon metachinjiensis* (Osborn, 1929) Chen, 2021, p. 25–26, fig. 13

Referred materials IVPP V2487 (Fig. 1A–B), left M3, from Ulanqab, Nei Mongol, precise locality is unknown; PIN 2202-4 and PIN 2202-5, left and right maxilla from the same individual with M2–M3, PIN 2202-6, left M3, from Middle Miocene of Tunggur region, Sonid Left Banner, Nei Mongol, (Dubrovo, 1970); IVPP RV74003 (Fig. 1C–D), left M3, from Jining, Ulanqab, Nei Mongol, precise locality is unknown; IVPP V4688.1 (Fig. 1E–F), complete left M3, from the Late Miocene Xiaolongtan Formation, Xiaolongtan coal mine, Kaiyuan, Yunnan; IVPP V4688.2 (Fig. 1G), posterior half of a right M3, IVPP V4685.7 (Fig. 1H) and V4685.8 (Fig. 1I), fragments of a left and a right M1, from the Late Miocene Xiaolongtan Formation, Yuxi coal mine, Yuxi, Yunnan; IVPP V5156 (Fig. 1J), fragmentary right M3 with the two anterior lophs, from Middle Miocene of Erlanggang, Fangxian, Hubei; IVPP V26802 (Fig. 1K–L), incomplete left m3, retaining the first three lophids, granted by the Daiyuan Primary School of Luonan County, Shaanxi Province, the precise locality is unknown.

Description M1 (IVPP V4685.7, Fig. 1H; V4685.8, Fig. 1I): the two specimens are deeply worn. The anterior and posterior pretrite crescentoids are developed, and the anterior

Table 1 Cheek teeth measurements of *Zygodolophodon* and *Miomastodon* (mm)

No.	Taxon	Specimen	L	W	W1	W2	W3	W4	Hpr(2)	Hpo(2)
IVPP V2487	<i>Z. cf. Z. turicensis</i>	left M3	190.97	92.11	81.89	92.11	84.65	73.45	61.55	55.87
RV74003	<i>Z. cf. Z. turicensis</i>	left M3	130.27	73.56	61.47	73.56	63.08	47.11	32.78+	41.56+
V4688.1	<i>Z. cf. Z. turicensis</i>	left M3	178.32	93.18	89.33	93.18	82.51	70.01	63.52	62.56
V26802	<i>Z. cf. Z. turicensis</i>	left m3	108.68+	72.91	72.92	72.01	64.76+		44.47+	27.37+
1986-NMG-DM	<i>Mio. gobiensis</i>	left m3	189.85	94.42	87.98	94.42	90.52	72.93	46.33+	58.27
1986-NMG-DM	<i>Mio. gobiensis</i>	right m3	187.84	96.95	90.48	96.95	91.78	72.04	41.21+	58.97
HMV1808	<i>Mio. gobiensis</i>	left m3	158.68	73.81	67.14	73.81	67.86	51.76	27.10+	35.25+
HMV1808	<i>Mio. gobiensis</i>	right m3	148.99	71.22	67.38	71.22	64.81	46.98	26.62+	39.83+
IVPP V26615	<i>Mio. gobiensis</i>	right m3	178.94	87.57	80.79	87.57	86.42			
HMV1938	<i>Mio. gobiensis</i>	right M3	147.18+	85.02	82.55	85.02	69.99	42.80		
HMV1939	<i>Mio. gobiensis</i>	right M2	129.56	85.11	77.18	82.41	85.11			
IVPP V26803	<i>Mio. gobiensis</i>	right M3	144.96	75.23	72.81	75.23	71.09	51.61	29.65+	47.02
IVPP V30715	<i>Mio. tongxinensis</i>	right M3	92.82+	79.14	79.14	73.06			49.80	47.76

Abbreviations: L, length of the crown; W, width of the crown; W1, 2, 3, 4, width at the 1st, 2nd, 3rd, and 4th loph(id); Hpr(2), high at the 2nd pretrite loph(id); Hpo(2), high at the 2nd posttrite loph(id).

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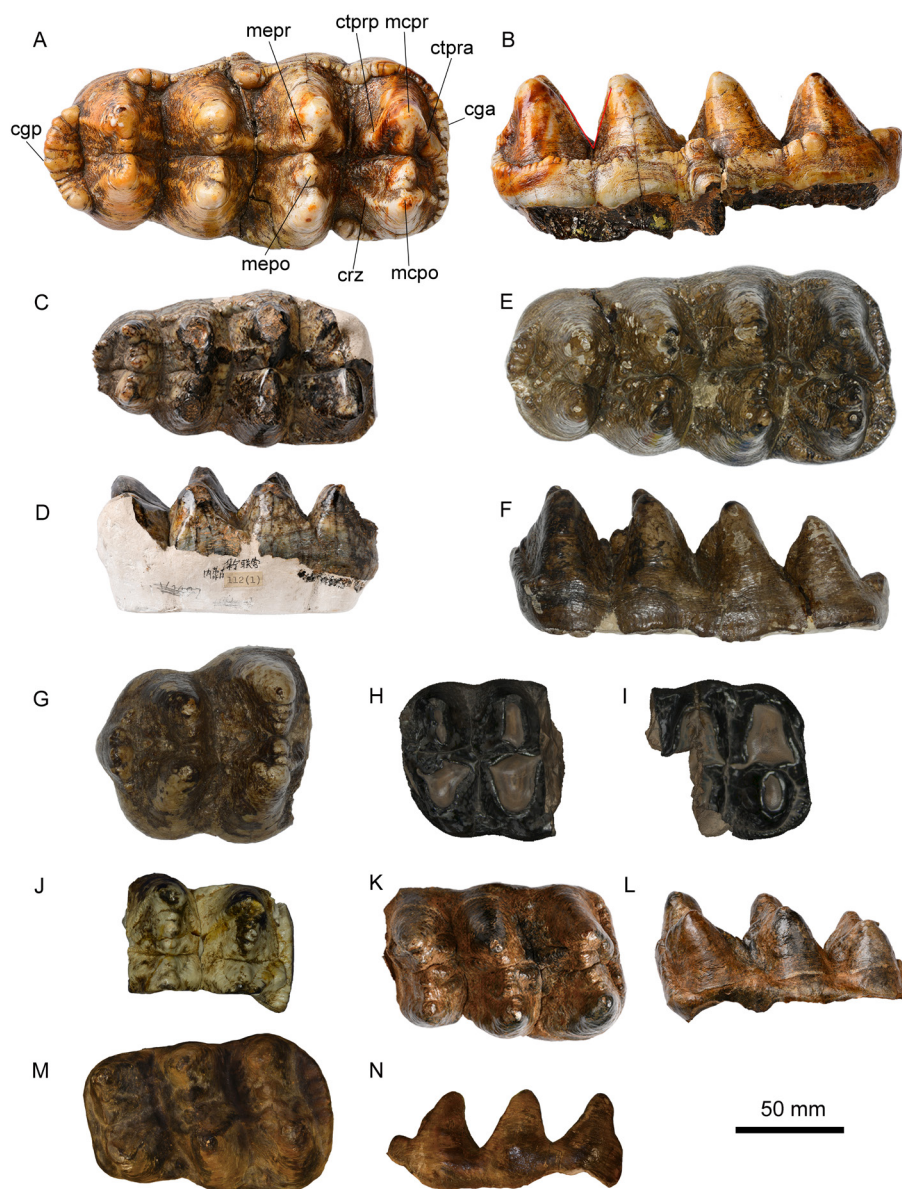


Fig. 1 Molars of *Zygodontophodon* cf. *Z. turicensis* and *Z. turicensis*

A–B. IVPP V2487, left M3 in occlusal (A) and lingual (B) views; C–D. IVPP RV74003, left M3 in occlusal (C) and lingual (D) views; E–F. IVPP V4688.1, left M3 in occlusal (E) and lingual (F) views; G. V4688.2, the posterior part of right M3 in occlusal view; H. V4685.7, anterior part of left M1 in occlusal view; I. V4685.8, posterior two lophs of right M1 in occlusal view; J. V5156, part of right M3 in occlusal view; K–L. V26802, left m3 in occlusal (K) and buccal (L) views; M–N. *Zygodontophodon turicensis*, NMB OSM1288 (type cast), left m2 in occlusal (M) and buccal (N) views

Abbreviations: cga, anterior cingulum; cgp, posterior cingulum; crz, zygodont crest; ctpa, anterior pretrite crescentoid; ctprp, posterior pretrite crescentoid; mcpo, posttrite main cusp; mcpr, pretrite main cusp; mepo, posttrite mesoconelet; mepr, pretrite mesoconelet

and posterior pretrite central conules are absent. The distal end of first posterior pretrite crescentoid is inflated, homologous to the posterior pretrite central conule. The posttrite half lophs are antero-posteriorly compressed and shows an approximately oval enamel ring due to deep wear. The anterior and posterior zygodont crests are developed. The interlophs are relatively narrow. Cingula are developed on the anterior and posterior margins of the tooth and the opening of interlophs on the pretrite side.

M3 (IVPP V2487, Fig. 1A–B; RV74003, Fig. 1C–D; V4688.1, Fig. 1E–F; V4688.2, Fig. 1G; V5156, Fig. 1J): the M3 is tetralophodont, and the second loph is the widest one. The pretrite main cusps are high and sharp. The anterior and posterior pretrite crescentoids and mesoconelets are crest-like, and the anterior and posterior pretrite central conules are absent. The posttrite main cusps are large, and the mesoconelets are subdivided. The zygodont crests are developed and thin crest-like. The second posterior pretrite crescentoids originate from the mesoconelets rather than from the main cusps. The interlophs are open. Cingula develop on the entire tooth crown margin except for the labial side. In lateral views, the lophs are “Λ-shaped”, the anterior and posterior pretrite crescentoids reach the bottom of the interlophs, and the interlophs are “V-shaped”.

The m3 (IVPP V26802, Fig. 2K–L): the lophids are oblique to the longitudinal axis. The pretrite main cusps are high and sharp. The anterior and posterior pretrite crescentoids and mesoconelets are crest-like. The posttrites are antero-posteriorly compressed, main cusps are high and sharp, and mesoconelets are subdivided. The zygodont crests are developed. The second anterior and posterior pretrite crescentoids originate from the mesoconelets. The second and third posttrites have weak anterior crescentoids. The interlophids are open, and cementum is absent. Cingulids are developed on the anterior margin of the tooth. In lateral views, the lophids are “Λ-shaped”. The first interlophid show a deep “V-shaped” sleeved by a shallow “V-shaped” and the second interlophid is deep “V-shaped”.

Genus *Miomastodon* Osborn, 1922

Type species *Miomastodon merriami* (Osborn, 1921)

Referred species *Mio. tongxinensis* Chen, 1978; *Mio. gobiensis* (Osborn & Granger, 1932); *Mio. metachinjiensis* (Osborn, 1929).

Diagnosis See Wang et al. (2020).

Miomastodon gobiensis (Osborn & Granger, 1932)

(Figs. 2, 3A–G; Tables 1, 2)

Type specimen AMNH 26461, a right hemimandible from Tunggur Formation, Tamuqin Fauna, late Middle Miocene, ~MN7/8 (Osborn and Granger, 1932; Wang et al., 2020).

Referred material HVM1939 (Fig. 3A), right M2, precise locality is unknown; HVM1938 (Fig. 3B), right M3, precise locality is unknown; IVPP V26803 (Fig. 3C), right M3, probably from the Dingjiaergou locality, Zhanghenbao Formation; 1986-NMG-DM (Fig. 2A–C, 4D), incomplete mandible, Damiao locality, Tunggur Formation; HVM1808 (Fig. 2D–E, 4G),

broken mandible with left and right m3, Laogou locality; IVPP V26615 (Fig. 3E–F), right m3, locality 86027, Tunggur Formation.

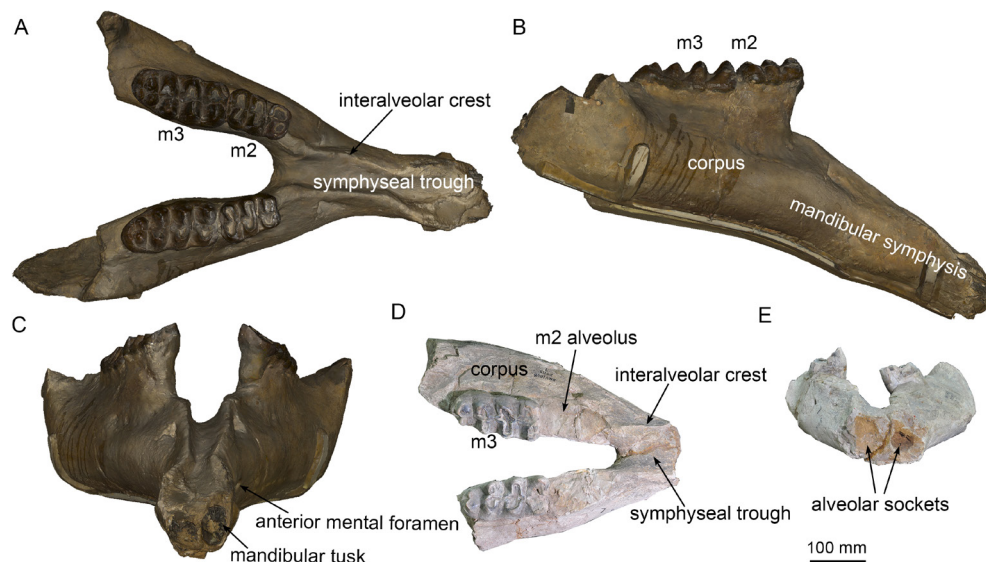


Fig. 2 Mandibles of *Miomastodon gobiensis*
A–C. 1986-NMG-DM in dorsal (A), lateral (B), and rostral (C) views;
D–E. HMV1808 in dorsal (D) and rostral (E) views

Description M2 (HMV1939, Fig. 3A): the first two pretrite half lophs show trifoliate patterns due to wear. The anterior and posterior pretrite crescentoids are strong. The first posterior pretrite and the second anterior pretrite central conules are present. The posttrite half lophs are antero-posteriorly compressed. The posttrite main cusps and the mesoconelets are indistinguishable, and the mesoconelets are subdivided and crest-like. The interlophs are open and a large amount of cementum developed. Cingula are developed on the antero-posterior and lingual side of crown.

M3 (HMV1938, Fig. 3B; IVPP V26803, Fig. 3C): the M3 is tetralophodont, but the fourth loph is less developed. The first two pretrite half lophs show trifoliate patterns due to wear, and the anterior and posterior crescentoids are strong. The distal end of the second anterior pretrite crescentoid is inflated like a central conule. The third anterior pretrite central conule is developed, and the posterior one is absent. The posttrite half lophs are antero-posteriorly compressed and show oval enamel rings under wear. The posterior zygodont crests are developed. The posterior two lophs are chevroned. The interlophs are open and cementum is developed. The cingula are weakly developed at the anterior and posterior margins of the crown.

Mandible (1986-NMG-DM, Fig. 2A–C): the mandible lacks the left and right rami. The mandibular tusks are broken from the opening of the incisive alveoli. The m2 is deeply worn with the anterior root being highly excavated from the alveolus. The m3 is moderately worn.

In dorsal view (Fig. 2A), the two corpora are moderately diverged in an angle of $\sim 30^\circ$.

The posterior end of the corpus is moderately widened relative to the anterior end, and the mandible is considerably constricted at the symphyseal part. The symphysis is relatively narrow and moderately elongated. The distal part of the symphysis is widened, stronger than that of the type specimen (AMNH 26461). The symphyseal trough is deep and bordered by the thick interalveolar crests. The caudal end of the symphysis is in line with the rostral end of the tooth row. The distal end of the symphysis exhibits an anteriorly oriented apex.

In lateral view (Fig. 2B), the mandibular corpus is restively high, with a thicker rostral end. The symphysis is anteriorly protruded with a downwardly deflection, which is stronger than that of the type specimen (AMNH 26461). There are three mental foramina, the caudal most one is small, at the level of the anterior end of the tooth row. A second one is larger, which is ~ 92 mm rostral to the first one, showing a rostral elongated groove. A third one is the rostral most mental foramen of the three. It is located at somewhat ventral of the symphysis (~ 113 mm rostroventral to the second one).

In rostral view (Fig. 2C), the symphyseal trough dips down rostrally showing a smooth and deep trough. The cross-section of the mandibular tusks is oval. The dorsoventral diameter

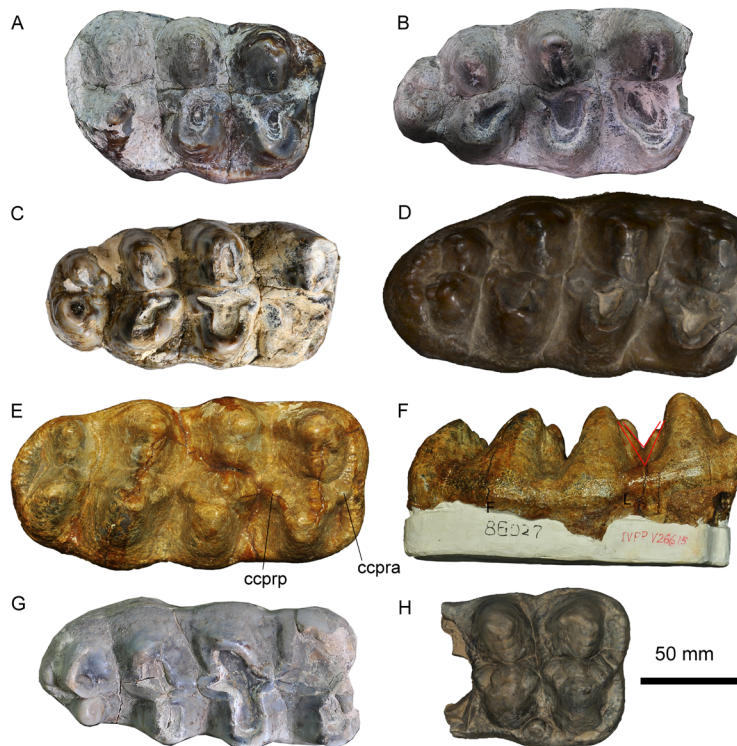


Fig. 3 Molars of *Miomastodon*

A–G. *Mio. gobiensis*: A. HMV1939, right M2 in occlusal view, B. HMV1938, right M3 in occlusal view, C. IVPP V26803, right M3 in occlusal view, D. 1986-NMG-DM, right m3 in occlusal view, E–F. IVPP V26615, right m3 in occlusal (E) and buccal (F) views, G. HMV1808, left m3 in occlusal view; H. *Mio. tongxinensis*, IVPP V30715, incomplete right M3 in occlusal view
Abbreviations: ccpra. anterior pretrite central conule; ccprp. posterior pretrite central conule

is larger than the mediolateral diameter, which we call the “erected oval cross-section”.

HMV1808 (Fig. 2D–E): the mandible lacks the left and right rami and the rostral end of the symphysis have been damaged. The left and right m2 alveolars were healing. The m3 is deeply worn, indicating that it belongs to an old individual. In dorsal view, the corpuses are anteriorly narrowed, the symphyseal trough is relatively wide, and the two interalveolar crests are parallel. The posterior edge of the symphysis is in a straight line with the front edge of the m2 alveolar. In rostral view, the two tusk alveolar sockets are deep, close to each other, and the cross-sections are round.

The m2 (1986-NMG-DM, Fig. 2A) is deeply worn. The lophids are gradually wider from anterior to posterior. The pretrite half lophids are trifoliate with a posterior lobe larger than the anterior one. The ectoflexid is U-shaped and the entoclexid possesses parallel borders. No accessory cusps rise from the posterior cingulid.

The m3 (1986-NMG-DM, Fig. 3D; IVPP V26615, Fig. 3E–F; HMV1808, Fig. 3G) is

Table 2 Measurements of the mandibles of *Miomastodon gobiensis*, after Tassy (2013) (mm)

	1986-NMG-DM	HMV1808
Length of preserved symphyseal	432.88	
Alveolar distance (from the most salient point of the trigonum retromolar to the symphyseal border of the corpus)	363.28	320+
Width of corpus measured at the anterioralveolus (or the grinding tooth if the alveolus is entirely resorbed)	120.51	70.32
Posterior symphyseal width	270.88	193.48
Maximum symphyseal width	136.04	
Minimum symphyseal width	114.64	160.85
Maximum width of rostral trough	100.40	
Minimum width of rostral trough	41.27	46.96
Internal width between anterior alveoli (or grinding teeth if the alveoli are resorbed)	116.78	72.20
Maximum height of corpus (measurement taken perpendicular to the ventral border of the corpus)	220.12	97.53
Height of corpus measured at the root of the ramus (measurement as above)	201.05	104.23
Rostral height measured at the symphyseal border (measurement taken perpendicular to the ventral border of the symphyseal rostrum)	176.71	99.28
Mid-alveolar length measured on the buccal side between the anterior alveolus (or grinding tooth if the alveolus is resorbed) and the root of the ramus	290.83	270

tetralophodont with thick enamel layer. The lophids are oblique to the longitudinal axis, and the first three lophids are equal in width. The pretrite and posttrite main cuspids are relatively high and large. The first pretrite and posttrite mesoconelets are subdivided and crest-like, but other pretrite and posttrite mesoconelets are less subdivided. The first anterior and posterior pretrite crescentoids are developed with papillary anterior and posterior pretrite central conules at the distal ends. The distal ends of the second anterior and posterior pretrite crescentoids are inflated, homologous to the central conules. Zygodont crests are developed. Cingulids are developed at the anterior and posterior margins of the crown. In lateral view, the lophids are “Λ-shaped”, but tips are blunter than *Z. turicensis*. The interlophids are stuffed up by the accessories (central conules and crescentoids), showing a deep “V-shaped” sleeved by a shallow “V-shaped” pattern.

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***Miomastodon tongxinensis* Chen, 1978**

(Fig. 3H; Table 1)

Type specimen IVPP V5584 (Chen, 1978: pl. II, fig. 2), a deeply worn right m3 from Zhangenbao Formation, Tongxin, Ningxia, late Early or early Middle Miocene.

Referred material IVPP V30715, an incomplete right M3, from the east cliff of the Dingshanyanchi Terrace, Junggar Basin, Xinjiang.

Description IVPP V30715 (Fig. 3H): the first loph is wider than the second one. The first pretrite half loph possesses a moderately developed mesoconelet. It has three aligned anterior central conules that links to the anterior cingulum. It also has a thick posterior crescentoid and a prominent posterior central conule. The second pretrite half loph possesses a slightly anteriorly displaced mesoconelet. The anterior and posterior crescentoids are weak, and the anterior and posterior pretrite central conules are equally developed. A posterior pretrite intermediate crescentoid is also present as in some specimens of *Mammutidae*. The posttrite half lophs are antero-posteriorly compressed. The first posttrite comprises three conelets. The outmost one represents the original main cusp and the inner two are subdivided mesoconelet. A weak anterior zygodont crest and a relatively strong posterior zygodont crest are present. Another two weak and crest-like posterior central conules are aligned with the posterior zygodont crest. The second posttrite half loph is similar to the first one. The zygodont crests and posterior central conules are weaker than those of the first posttrite, but additionally possesses a crest-like anterior posttrite central conule. The cingula are strong. In lateral view, the interloph show a deep “V-shaped” sleeved by a shallow “V-shaped” pattern.

3 Comparison and discussion

Many species under the genus *Zyglorhodon* had been established in China. Osborn and Granger (1932) reported a right hemimandible from Tunggur, Nei Mongol, and identified it as *Serridentinus gobiensis*. The genus *Serridentinus* should belong to a bunodont type and has been synonymized with *Gomphotherium*. Tobien (1972) considered that the tooth morphology is closer to the zygodont mastodonts. Tassy (1985) identified another mandibular fragment with m3 in the AMNH collections from Tunggur as *Z. gobiensis*. Chow and Chang (1961) reported an M3 from Miocene of Nei Mongol and erected the species, *Zyglorhodon (Turicus) nemonguensis*. Dubrovo (1970) reported a left and a right upper maxilla belonging to the same individual and a left M3, all from the Middle Miocene of Tunggur, Nei Mongol, and erected the species of *Z. gromovae*. Chow and Chang (1974) reported a left M3 from the Miocene of Jinjing, Nei Mongol, and erected the species of *Zyglorhodon (Turicus) jiningensis*. Chow et al. (1978) reported three specimens from the Late Miocene of the Xiaolongtan Formation, Yunnan, and identified as *Z. chinjiensis*. Yan (1979) reported a fragment of m3 from the Middle Miocene of Fangxian, Hubei Province, and identified it as *Z. nemonguensis*. Tobien et al. (1988) synonymized all the Chinese zygodont proboscideans with one species *Z. gobiensis*.

Besides the materials listed above, they also included *Mio. tongxinensis* from Tongxin, Ningxia, published by Chen (1978), and two specimens of *Gomphotherium xiaolongtanensis* from Xiaolongtan, Kaiyuan, Yunnan, published by Chow et al. (1978). The type specimen was assigned as the mandible (AMNH 26461) of *Z. gobiensis*. Chen (2021) believed that there are more than one species of *Zygodontophodon* in China, and some materials may not belong to *Z. gobiensis*, such as *Mio. tongxinensis*. However, she still insisted on grouping them into one genus, and did not compare the materials discovered in recent years.

It has long been noticed that two tooth morphic-types are present in mastodont proboscideans, the bunodont and zygodont types, representing the two major branches of elephantimorph, Gomphotheriidae and Mammutidae. Morphology of zygodonty occurred at a very early stage of elephantimorphs, i.e., the Early Oligocene, represented by *Palaeomastodon* (Matsumoto, 1924; Tobien, 1978; Madden, 1980; Sanders et al., 2004). The Late Oligocene *Losodokodon* had been an entirely zygodont elephantimorph (Rasmussen and Gutierrez, 2009). However, intermediate tooth morphology forms are co-existed with typical bunodonts and zygodonts continuously during the Late Neogene, which has made difficulties in the taxonomy of related taxa. For example, in Europe, *G. subtapiroideum* obfuscates the boundary between *G. angustidens* and *Z. turicensis* (Schlesinger, 1917; Lehmann, 1950; Mazo, 1996; Göhlich, 1999; Radović and Bradić-Milinović, 2018); in Asia, *Serridentinus gobiensis* and *S. metachinjiensis* were transferred to *Zygodontophodon* (Tassy, 1985; Tobien, 1996).

According to Tassy (1985), the *Z. turicensis* in Europe contains both robust (intermediate morphology) and gracile (typical zygodont) types and he mentioned that the molars of AMNH 26461, the type hemimandible of *Serridentinus gobiensis* represents the robust type. Tobien et al. (1988) also pointed out that AMNH 26461 corresponds to the robust types and *Z. gromovae* corresponds to gracile types. Recently, Wang et al. (2020) further attributed these Asian robust types to *Miomastodon*. Tobien et al. (1988) mentioned that the gracile zygodont specimens from China are smaller in size than *Z. turicensis* from Europe, and sometimes, no pretrite mesoconelets are present. However, these differences do not seem to be enough to re-establish a new species, and the size of upper M3 (IVPP V2487, *Z. (Turicus) nemonguensis*) from Nei Mongol is rather large. The type specimen of *Z. turicensis* (Fig. 1M–N) is an m2 from the Middle Miocene near Zurich, Switzerland. The lophids are sharp. The anterior and posterior crescentoids are thin. The central conules are absent. The interlophids are open and “V-shaped” in lateral views. Compared with the type specimen, the above-mentioned Chinese gracile type materials exhibit the same degree of zygodonty, which corresponds to the European gracile type *Z. turicensis* described by Tassy (1985). Therefore, here, Chinese gracile type zygodonts are attributed to *Zygodontophodon*, and identified as *Zygodontophodon* cf. *Z. turicensis*.

The earliest known *Zygodontophodon* is *Z. aegyptensis* from the Early Miocene, about 18.0–17.0 Ma ago, in Moghara, Egypt (Sanders and Miller, 2002). Compared with *Z. aegyptensis*, *Zygodontophodon* cf. *Z. turicensis* is larger in size, has a better-developed fourth loph, and the third loph of M3 is not convex in the median sulcus, and shows a higher degree

of zygodonty. Another species of *Zygodontophodon* is *Z. atavus* from the Early Miocene Jilančik beds of Kazakhstan, central Asia (Borissiak, 1936). The mandibular symphysis is longer than *Z. turicensis* (Březina, 2014; Sanders and Miller, 2002). The two mandibular tusks are relatively developed and close to each other, and the cross-section has a larger mediolateral diameter than dorsoventral diameter. The dimensions of the m3, and the width-length ratio of the first two lophids fall into the ranges of *Zygodontophodon* (Wang et al., 2020). Due to its early age (Early Miocene), *Z. atavus* may represent a more primitive feature of *Zygodontophodon*. Apparently, *Zygodontophodon* cf. *Z. turicensis* from China is more progressive in morphology with later ages.

The incomplete mandible (1986-NMG-DM) recovered from the late Middle Miocene of the Damiao locality, Nei Mongol, shows intermediate tooth morphology between Gomphotheriidae and Mammutidae, which belongs to the robust zygodont types. The pretrite crescentoids are thick and the central conules are present. The posttrite half lophids are antero-posteriorly compressed, and the interlophids are open. In addition, the mandibular symphysis is relatively narrow and moderately elongated. The cross-section of the mandibular tusk is erected oval. These characters are in accordance with the diagnosis of *Mio. gobiensis*. It slightly differs from the type hemimandible (AMNH 26461) in the more ventrally bend of symphysis, and the more lateral expansion in the distal symphysis. These differences were treated as intraspecific variations here.

The mandible (HMF1808) was excavated from the same locality as the *Mio. gobiensis* cranium (GPM ZR001141) (Li Y et al., 2021). Like the type specimen of *Mio. gobiensis* (AMNH 26461), the hemimandibles of HMF1808 also taper rostrally and the symphyseal trough is smooth. Observing from the alveolar of the mandibular tusks, the left and right mandibular tusks are also rod-shaped and close to each other. Although the m3 is deeply worn, the lophids are weakly antero-posteriorly compressed, the anterior and posterior crescentoids are strong, and the anterior and posterior pretrite central conules are present. According to the above morphological characteristics, it is reasonable to classify HMF1808 to *Mio. gobiensis*. On the two deeply worn upper molars (HMF1938, M3; HMF1939, M2), the lophids are less sharp, the anterior and posterior crescentoids are strong and distal inflated, indicating the anterior and posterior pretrite central conules are developed, and the posttrite half lophids are less subdivided compared to the typical zygodonts. The third loph of M3 is chevroned. These two molars are very similar to M2 and M3 on the cranium of *Mio. gobiensis* (GPM ZR001141), and hereby were attributed to the same species.

On the complete right m3 (IVPP V26615) from Nei Mongol, the lophids are slightly antero-posteriorly compressed and blunt in lateral views, the anterior and posterior pretrite central conules are developed, the posttrite half lophids are moderately subdivided, and the interlophids show patterns of a deep “V” sleeved a shallow “V” in lateral views. The above features meet the diagnosis of *Mio. gobiensis*.

Although the right M3 (IVPP V26803) from Tongxin is deeply worn, the retained features show that the lophids are slightly antero-posteriorly compressed, the anterior and posterior

crescentoids are strong, the posttrites are moderately subdivided, and the zygodont crests are weak. So, it is reasonable to be classified as *Miomastodon*. This specimen was discovered from Dingjiaergou, Zhangebao Formation in the Tongxin region, Ningxia, but the stratigraphic position is higher than IVPP V5584, type specimen of *Mio. tongxinensis*. Compared with the V5585, the same individual as the V5584, the fourth loph of V26803 is more developed, the second anterior and posterior pretrite crescentoids are thicker, and the second posterior pretrite central conule is more obvious and larger. Therefore, we attributed specimen of Dingjiaergou to *Mio. gobiensis*.

The incomplete right M3 (IVPP V30715) was broken from the second interloph. However, the first two lophs are complete. Chen (1988) reported two jaws with M2–M3 from Botamoyin of the Halamagai Formation. She established a new species, “*zunggarensis*”, and doubtfully attributed it to *Zygodontophodon*. Chen (2021) further attributed them to *Zygodontophodon* and identified as *Z.? zunggarensis*. However, these specimens cannot be found currently, and the attribution of “*zunggarensis*” remains a problem. Wang et al. (2020) temporarily attributed them to *Miomastodon* sp. and mentioned that it might be close to *Mio. tongxinensis*. The specimen V30715 was recovered from the same horizon as the hypodigm of *Z.? zunggarensis* in 2021, and the absolute age is about 16 Ma (Ye et al., 2012), close to *Mio. tongxinensis* from Tongxin region. On the second loph of V30715 and V8583 (Chen, 1988:270–273, pl. IV, fig. 3), the anterior and posterior pretrite crescentoids are weaker but the pretrite central conules are obvious and rather large, similar to V5585 (*Mio. tongxinensis*, Chen, 1978:pl. II, fig. 1). Therefore, here we referred V30715 to *Mio. tongxinensis*.

We further compare the tooth dimensions of some zygodont proboscideans from China (Fig. 4). The M3 (RV74003, *Z. jiningensis*) from the Miocene (?) of Jining is the smallest and

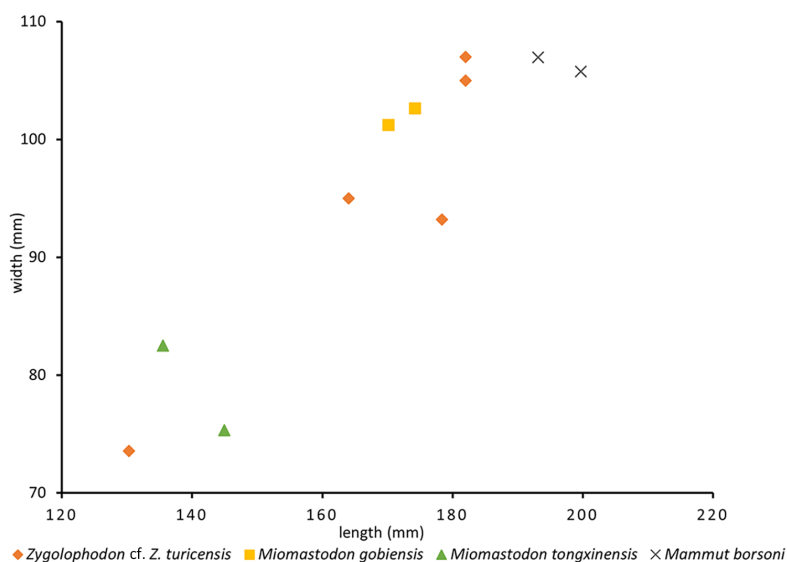


Fig. 4 Scatter diagrams comparing the dimensions of M3 (lengths and widths max.) in several species of zygodont proboscideans from China

probably one of the earliest representatives of the Chinese *Zygodont*. The type M3 of *Z. (Turicus) nemonguensis* is the largest *Zygodont* currently found in China. In terms of species, the M3 of *Mio. tongxinensis* is smaller than other zygodont proboscideans, and *Mio. gobiensis* is in a similar width-length proportion to *Zygodont* cf. *Z. turicensis*. But all the zygodonts from Miocene is smaller than *Mammuth borsoni* in China.

4 Geographical distribution of zygodonts in China

Zygodont was discovered from Tunggur and Jining of Nei Mongol, Luonan of Shaanxi, Fangxian of Hubei, Yuxi and Xiaolongtan of Yunnan in China. *Z. gromovae* was discovered from the Middle Miocene Tunggur, Nei Mongol. *Z. (Turicus) nemonguensis* and *Z. gromovae* obviously belong to typical gracile type zygodonts (Dubrovo, 1970, 1974; Duangkrayom et al., 2017). The left m3 from Luonan County, Shaanxi Province, although only the front three lophids are retained, also belongs to typical gracile type zygodonts. Another material that has been identified as *Z. (Turicus) nemonguensis* is the fragmentary of M3 (IVPP V5156) from Fangxian, Hubei. According to the features of the preserved part, it is slightly more primitive than the type specimen of *Z. (Turicus) nemonguensis*, and it has the precise location. According to Deng et al. (2019), the Fangxian locality belongs to the Tunggurian, Middle Miocene. So, it is speculated here that the age of the type specimen may be the same as the Fangxian material or slightly later. Other materials classified as *Zygodont* cf. *Z. turicensis* are from the Xiaolongtan Formation in Yunnan, including *Z. chinjiensis* and two specimens of “*Gomphotherium xiaolongtanensis*”. In previous studies, such as Deng et al. (2019) and Li et al. (2015), the age of the Xiaolongtan Formation belongs to the Middle Miocene. But according to the latest research of Li C et al. (2021), the Xiaolongtan Formation may belong to the early Late Miocene. Therefore, *Zygodont* cf. *Z. turicensis* in China might cover from the late Early or early Middle Miocene (possibly from Jining) to the end of the Middle Miocene of northern China, and further extend to the south China in the early Late Miocene. Duangkrayom et al. (2017) reported the first record of *Zygodont* from the Late Miocene in Tha Chang, Thailand, Southeast Asia, indicating that *Zygodont* did not enter the lower latitudes until the Late Miocene. The *Zygodont* specimens in Tha Chang might represent a dispersal link between South and East Asia during the Middle and Late Miocene. The *Zygodont* cf. *Z. turicensis* specimens from China further supported this view.

Miomastodon was discovered from Tongxin of Ningxia, Junggar Basin of Xinjiang, Linxia Basin of Gansu, and Tunggur region of Nei Mongol (Wang et al., 2020; Li Y et al., 2021). Both *Miomastodon* and *Zygodont* were found in the Middle Miocene of northern China. Whereas *Zygodont* is rare and sporadically distributed, although it appeared in the southern China during the early Late Miocene. In China, *Miomastodon* was the predominant member of Mammutidae during the Early and Middle Miocene and only found in northern China. The ancestral species is *Mio. tongxinensis*, which possibly spanned approximately 17–14 Ma of the

late Early to early Middle Miocene of Tongxin (Li et al., 2023) and Junggar Basin. The derived species, *Mio. gobiensis*, is distributed in the late Middle Miocene of Linxia and Tunggur basins.

The type locality of *Mio. merriami* is Virgin Valley, McGee, Humboldt Co., Nevada, North America, early Barstovian (15.18–15.84 Ma) (Osborn, 1921; Koenigswald et al., 2021). However, the age of *Gomphotherium* spreading from Eurasia to America is ~16 Ma (Qiu, 2003), indicating that at least in the early Middle Miocene, the Mammutidae, represented by *Miomastodon*, from Eurasia had entered North America along with *Gomphotherium*.

A cladistic analysis was carried out to clarify the phylogenetic positions of Mammutidae from China (Fig. 5). Since the materials of *Eozygodon* sp. and *Zygodon* cf. *Z. turicensis* are scarce, we added two species, *Eozygodon morotoensis* and *Z. turicensis*. On this basis, we proposed evolutionary relationships and geohistoric distribution of species of the family Mammutidae in China (Fig. 6). According to Fig. 6 and Zhang and Wang (2021), *Miomastodon* show a higher degree of zygodondy than *Eozygodon*. In China, *Zygodon* might derived from *Eozygodon* and further gave rise to *Mammut*.

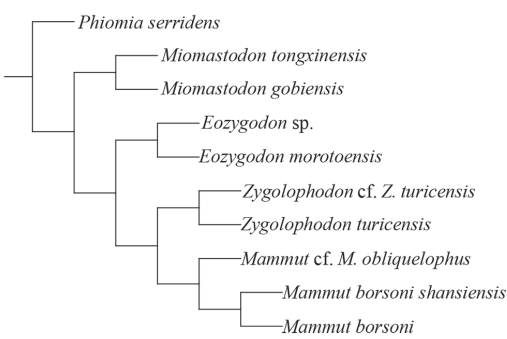


Fig. 5 Cladistic analysis of the family Mammutidae The cladistic analysis is performed using TNT v.1.1 and new technology search, based on the characters provided in Appendix 1 and the data matrix in Appendix 2; CI (consistency index) = 0.807, RI (retention index) = 0.653

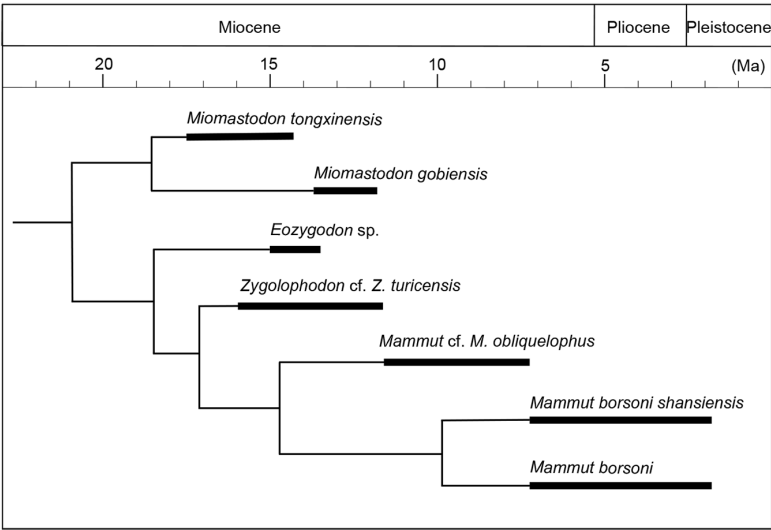


Fig. 6 Proposed evolutionary relationships and geohistoric distribution of species of the family Mammutidae in China

5 Conclusions

In the present paper, we comprehensively studied the old and new specimens of *Zygodontodon* and *Miomastodon*. The specimens attributed to *Zygodontodon* shows a high degree of zygodonty that is strongly comparable with the type species, *Z. turicensis*, from the Middle and Late Miocene of Europe. Whereas the other specimens from Early and Middle Miocene of northern China show a relatively low degree of zygodonty and can be attributed to *Miomastodon*. Two species, *Mio. gobiensis* and *Mio. tongxinensis* were identified. In the Early and Middle Miocene, *Miomastodon* was the predominant member of Mammutidae in northern China, and at least in the early Middle Miocene, *Miomastodon* entered North America. *Zygodontodon* evolved from *Eozygodon* and further evolved into *Mammut* in China.

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Supplementary file can be found on the website of Vertebrata Palasiatica (<http://www.vertpala.ac.cn/EN/2096-9899/home.shtml>) in Online First.

中国中新世颊齿象类新材料及有关分类厘定

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摘要: 中国中新世的颊型齿长鼻类化石虽然分布广泛, 但材料稀少, 分类上经历了从多个颊齿象(*Zygodontodon*)种到全部归为戈壁颊齿象(*Zygodontodon gobiensis*)一个种的状态。戈壁颊齿象既包含颊型化程度较高的纤细型也包含介于颊型齿和丘型齿中间的粗壮型。最近, 随着粗壮型被归入中新乳齿象属(*Miomastodon*)以及新材料的发现, 有必要对中国中新世的颊齿象类进行重新厘定。结合已知的纤细型颊齿象颊齿材料和新发现的玛姆象科(Mammutidae)材料, 对中国中新世颊齿象类材料进行研究, 认为颊型化程度较高的纤细型种类包括内蒙古颊齿象(*Z. nemonguensis*)、格氏颊齿象(*Z. gromovae*)、集宁

軛齿象(*Z. jiningensis*)、庆义軛齿象(*Z. chinjiensis*)以及归入小龙潭嵌齿象(*Gomphotherium xiaolongtanensis*)的两件标本,都应该归入传统意义上的軛齿象属,因为它们臼齿齿脊尖锐,主齿柱前后新月嵴成细嵴状,中心小尖消失或发育很弱,副齿柱中附锥分裂,軛齿嵴发育,侧视齿柱呈A形,齿谷V形,这些零散的颊齿形态与欧洲苏黎世軛齿象(*Z. turicensis*)正型标本相似,由于材料比较缺乏,暂将其归为苏黎世軛齿象相似种(*Zygodolophodon* cf. *Z. turicensis*)。来自甘肃和政、内蒙古通古尔、宁夏同心和新疆准噶尔的新材料,軛型化程度较低,对应于介于軛型齿和丘型齿之间的粗壮型,将其分别归入中新乳齿象属的戈壁种(*Miomastodon gobiensis*)和同心种(*M. tongxinensis*)。与戈壁种相比,同心种的臼齿主齿柱前后新月嵴发育更弱,前后中心小尖更大。地质时代及地理分布表明,早中新世至中中新世中国北方的軛齿象类主要以*Miomastodon*为主。新材料的发现和对整个軛齿象类的重新厘定,为玛姆象类从欧亚大陆向北美的扩散以及在中国本土的演化提供了证据。

关键词: 中国, 中新世, 玛姆象类, 軛齿象属, 中新乳齿象属

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